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Long-term partial cutting impacts on *Desmognathus* salamander abundance in West Virginia headwater streams

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Abstract

To understand long-term impacts of partial cutting practices on stream-dwelling salamanders in the central Appalachians, we examined pooled abundance of *Desmognathus* fuscus and *D. monticola* salamanders (hereafter *Desmognathus*) in headwater streams located within long-term silvicultural research compartments on the Fernow Experimental Forest, Tucker County, West Virginia. We sampled *Desmognathus* salamanders in 12 headwater streams within silvicultural research compartments that have been subjected to partial cutting for approximately 50 years. We used an information-theoretic approach to test five *a priori* models explaining partial cutting effects at the compartment-level on *Desmognathus* abundance and eight *a priori* models explaining stream reach-scale habitat effects on *Desmognathus* abundance. Our modeling efforts resulted in the selection of two competing models explaining partial cutting effects on *Desmognathus* abundance at the compartment-level. The VOLUME model, which incorporated cumulative timber volume harvested within compartments, received the greatest support and indicated that *Desmognathus* abundance was impacted negatively by increased timber volume removal. The second model, LASTDISTURB, incorporating the single variable of time since last harvest activity, indicated that *Desmognathus* abundance increased with time since last harvest at the compartment-level. For stream reach-scale habitat variables, the EMBEDDED model incorporating the percent of embedded substrate within streams, received the strongest support for explaining *Desmognathus* abundance. Our results suggest that long-term partial cutting suppresses *Desmognathus* abundance, possibly by increasing stream sedimentation and thereby reducing available cover for juvenile and adult salamanders. However, these practices do not appear to have threatened long-term persistence of *Desmognathus* in central Appalachian headwater streams.

Keywords: Best management practices; Central appalachians; Desmognathus; Forest management; Headwater streams; Partial cutting; Sedimentation

1. Introduction

In the eastern United States, stream salamanders are the most numerically abundant vertebrates in most headwater streams, often replacing fish as top predators (Petranka, 1983; Hairston, 1987; Lowe and Bolger, 2002). Because of their abundance and high trophic level position, these salamanders serve as keystone predators, thereby exerting disproportionate influence on biotic community structure in headwater stream habitats (Davic and Welsh, 2004). Although many species frequently forage in surrounding non-aquatic riparian areas (Petranka and Smith, 2005), aquatic habitats for breeding, larval growth, and refugia are necessary for survival (Petranka,

1998). Accordingly, aquatic salamanders often are sensitive to stream habitat alterations resulting from upland watershed disturbances, such as timber harvesting. Despite the importance of aquatic habitats for cover and reproduction, investigations of partial cutting impacts in the Central and Southern Appalachian Mountains have primarily focused on terrestrial environments (Harpole and Haas, 1999; Ford et al., 2000, 2002; Duguay and Wood, 2002; Knapp et al., 2003). These studies suggest that partial cutting practices somewhat adversely affect salamander capture rates and population demography, at least in the shortterm. In New England, Lowe and Bolger (2002) observed that Gyrinophilus porphyriticus density in headwater streams increased with increasing time since last harvest disturbance (e.g., clearcutting, commercial thinning, single-tree selection, and group selection). Also, Perkins and Hunter (2006) found Eurycea bislineata exhibited a trend of decreasing abundance with increasing harvest intensity within streams adjacent to

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riparian areas subject to partial cutting 4-10 years prior to sampling, clearcut with 35 m forested buffers along streams, and unmanipulated mature forest (>50 years since last harvest). Upland harvesting activities can negatively alter stream habitat components important to aquatic salamander species (de Maynadier and Hunter, 1995; Corn et al., 2003). Soil disturbance, skid road creation, and removal of streamside vegetation can increase stream siltation and stream temperature in the short-term (Reinhart et al., 1963; Patric, 1980; Kochenderfer et al., 1987), possibly reducing cover sites important to stream salamanders by filling interstitial spaces (Bury and Corn, 1988; Corn and Bury, 1989; Lowe and Bolger, 2002; Lowe et al., 2004). The degree to which streams are impacted, and subsequently recover, depends on a variety of factors including harvesting intensity and frequency, and road density within watersheds (Aubertin and Patric, 1974; Stuart and Edwards, 2006). Water quality measures outlined in many state best management practice (BMP) guidelines, such as retention of forested buffer zones and proper skid and logging road placement, can help mitigate many adverse timber harvesting effects on stream habitats (Kochenderfer et al., 1997; Kochenderfer and Edwards, 1990). However, because partial cutting practices often involve periodic timber removal operations every 10-20 years (Smith et al., 1997), repeated harvesting may produce chronic sedimentation effects that reduce stream habitat quality for aquatic salamanders. In the central Appalachians, Knapp et al. (2003) suggested that if salamander populations do not recover following partial cutting to precutting levels before successive cuts then populations may never reach precutting levels and could remain suppressed in the long-term.

A better understanding of how stream salamander populations are affected by partial cutting is needed as many regions in the eastern United States are experiencing increased timber harvesting following maturation of second- and third-growth forests. Public concern over clearcut harvesting effects on wildlife habitat and aesthetics has, in part, prompted increased use of partial cutting practices, such as single-tree selection, patch cutting, and diameter-limit cutting, regardless of ownership. For both public and privately owned forests, partial cutting practices provide a continuous canopy cover, thereby enhancing aesthetic value, and satisfies economic objectives by generating periodic financial returns throughout the rotation (Miller, 1993). Currently, partial cutting is the most commonly practiced harvesting method on non-industrial private forests (NIPF) in the central Appalachians (Fajvan et al., 1998; Fajvan, 2006). Because NIPF account for the majority of commercially utilized forestlands in the East, the effects of timber harvest practices implemented on these forests have important consequences for wildlife conservation in the region (Fredericksen et al., 2000).

To determine cumulative effects of partial cutting practices on stream salamanders in the Allegheny Mountain region of the central Appalachians in West Virginia, we examined the pooled abundance of *Desmognathus fuscus* and *D. monticola* salamanders (hereafter *Desmognathus*) in headwater streams within long-term silvicultural research compartments that have been subjected to repeated partial cutting over the past 50 years.

The long life span, small home ranges, and limited dispersal ability of Desmognathus (Barbour et al., 1969; Barthalamus and Bellis, 1972) makes them well-suited as indicators of disturbance in forested landscapes (Welsh and Ollivier, 1998; Welsh and Droege, 2001). Accordingly, our objective was to determine how repeated partial cutting over an approximate 50year period affected *Desmognathus* abundance. Specifically, we examined (1) the influence of variables associated with partial cutting on *Desmognathus* abundance within adjacent headwater streams and (2) the importance of reach-scale stream variables in determining *Desmognathus* abundance. We hypothesized that Desmognathus abundance within sampled streams would decrease with increased amount of cumulative timber volume removed. In addition, we hypothesized that stream reaches with greater sedimentation impacts, such as greater percentages of fine sediments and embedded substrate, would exhibit reduced *Desmognathus* abundance.

2. Study site and methods

2.1. Site description

We conducted our study on the Fernow Experimental Forest (FEF) in Tucker County, West Virginia. The FEF is a 1902-ha experimental forest located wholly within the Unglaciated Allegheny Mountains subsection of the Appalachian Plateau Physiographic region. Broad ridge tops, narrow valleys, steep side-slopes ranging from 10 to 60%, and high-gradient streams characterize the topography of the FEF. Soils are predominantly of the Calvin and Dekalb series originating from sandstone parent material or the Belmont series originating from limestone parent material. All types are well-drained, medium-textured loams and silty loams, with an average depth of 1 m. The climate is cool and moist with mean annual precipitation approximating 145 cm and being evenly distributed throughout the year. Elevations range from 533 to 1112 m. Forest cover is primarily second-growth mixed mesophytic hardwood type consisting of sugar maple (Acer saccharum), red maple (A. rubrum), northern red oak (Quercus rubra), chestnut oak (O. prinus), yellow-poplar (Liriodendron tulipifera), American beech (Fagus grandifolia), sweet birch (Betula lenta), black cherry (Prunus serotina), and basswood (Tilia americana; Madarish et al., 2002). The majority of the FEF initially was logged between 1903 and 1911. In the 1930s approximately 25% of the standing tree volume was reduced as a result of chestnut blight (Cryphonectria parasitica) (Trimble, 1977). The FEF is managed by the USDA Forest Service's Northern Research Station for long-term silvicultural watershed and ecological research (Schuler and Gillespie, 2000). Research stands on the FEF are managed using a variety of silvicultural practices including even-aged, patch cutting, diameter-limit, and uneven-aged single-tree selection.

2.2. Methods

We identified 12 silvicultural research compartments, ranging in size from 13 to 73 ha, that had been subjected to

partial cutting practices over an approximate 50-year period. Partial cutting treatments represented a range of intensities commonly employed in the Central Appalachian Mountain region. Cutting practices included: Patch Cutting (n = 3): Stands subject to patch cutting with initial cuts between 1955 and 1958 with the last harvest entry 5–8 years prior to sampling; cumulative harvest volume ranged from 109 to 149 m³/ha. Patch cutting involved removing all stems >2.54 cm diameter at breast height (DBH) within 0.16 ha circular plots covering about 12% of the stand during each cutting cycle of 10-15 years; Single-tree selection (n = 4): Stands subject to singletree selection with initial cuts between 1950 and 1958 with the last entry 2-14 years prior to sampling; cumulative harvest volume ranged from 52 to 137 m³/ha; and *Diameter limit* harvesting (n = 1): Diameter-limit harvesting involved removal of all trees >46 cm DBH with the last harvest entry 7 years prior to sampling; cumulative harvest for the diameter limit compartment was 78 m³/ha. Additionally, we sampled four compartments containing mature second-growth stands logged during the initial exploitative harvesting in the early 20th Century (Trimble, 1977) but that have not been subjected to any further cutting. See Schuler (2004) for further details regarding treatment descriptions. We measured road density within compartments using ArcView 3.8 software (ESRI, Redlands, California). Road densities ranged from 0 to 35.5 m/ha.

We sampled small, perennial headwater streams ($\leq 2.5 \text{ m}$ width) within each compartment between June and August 2005 by establishing three, 10 m reaches at the upper, middle, and lower portions of the stream separated by 50 m or greater. Sampled streams fell completely within silvicultural research compartments. Reaches ranged in elevation from 593 to 810 m. Prior to salamander sampling within each reach, we randomly six "unoccupied" cover objects at least $16 \text{ mm} \times 16 \text{ mm}$ within the streambed by selecting two numbers from a random numbers table to serve as coordinates with the bank serving as the x-axis and the bottom portion of the stream reach as the y-axis (Smith and Grossman, 2003). We selected an alternative cover object if the random site was occupied by a salamander. We placed a 0.5 m² plot over each randomly selected cover object and ocularly estimated percent substrate size class (fine substrate <2 mm, gravel 2–16 mm, cobble >16–256 mm, and boulder >256 mm; Allan, 1995), cover type (rock, debris, coarse woody debris), percent water, percent water class (pool, riffle, run), and percent embedded rock (percentage of the vertical surface of substrate buried in sand or silt). We classified sand and silt together as fine sediment (Gordon et al., 1992). Stream width was measured at 5 m intervals within each 10 m reach (n = 3). Percent slope was recorded for each reach using a clinometer (Suunti, Vantaa, Finland) and water pH was estimated using a pH51 meter (Automated Aquarium Systems, Tustin, California). We measured basal area along each reach by establishing a 10 m × 10 m plot along each bank. Diameter at breast height was recorded for trees >7.5 cm in each plot.

We systematically searched the streambed of each reach by overturning cover objects greater than $16~\text{mm} \times 16~\text{mm}$ and raking the substrate. We identified captured salamanders to

species. Because it is often difficult to capture every salamander uncovered, individuals were first identified to genus before making any capture attempt to ensure that as many individuals as possible located within the reach were recorded. Microhabitat data was not recorded for uncaptured individuals. We recorded length (cm) and width of cover objects where salamanders were captured and aforementioned habitat variables within 0.5 m² plots at each cover object location. We recorded habitat variables for each occupied site immediately following capture of an individual to minimize search disturbance effects on stream microhabitat variables. Neither brook trout (*Salvelinus fontinalis*) or any other species of fish were present in sampled streams (K. Hartman, Personnel Communication, West Virginia University, Division of Forestry and Natural Resources).

2.3. Statistical analyses

We tested assumptions of normality for salamander abundance data and all habitat measures at the compartment-level (n = 12) and stream reach-scale (n = 36) using the Shapiro-Wilks test (Sokal and Rohlf, 1987). Because only a certain proportion of a salamander population is active on the surface during a given period, our abundance estimates are only a relative measure of actual salamander population abundance within streams. However, surface captures are often significantly correlated with mark-recapture abundance estimates (Smith and Petranka, 2000). All proportional variables were arcsin square-root transformed prior to analysis (Sokal and Rohlf, 1987). If variables still deviated from normality following transformation, we performed analysis on ranked data. Untransformed values for stream-reach variables are reported (Table 1). To identify broad habitat use patterns for *Desmognathus* at the reach-scale we pooled microhabitat variables recorded for D. fuscus and D. monticola. We calculated means for occupied and unoccupied microhabitat variables in each reach and then compared them using two sample *t*-tests (n = 36). We set the significance level for all tests at $\alpha = 0.05$. We performed all statistical analyses using SAS v 9.1 (SAS[®], 2003).

Because stream widths were similar among sampled streams (Analysis of variance; $F_{11.24} = 0.42$, P = 0.935) and salamander abundance was not influenced by stream width (Spearman's rank; $r_s = -0.05$, P = 0.76) we analyzed reach-scale and compartment-level effects on total salamander abundance. We examined the relation between abundance of Desmognathus with compartment-level cutting disturbance variables (n = 12) and reach-scale habitat variables (n = 36) with a series of linear regression models in an information-theoretic approach. We used Akaike's Information Criterion corrected for small sample size (AICc) as overall sample size divided by total parameter units examined was <40 (Burnham and Anderson, 2002). Prior to model selection, we examined fit of global models following recommendations of Burnham and Anderson (2002). We constructed a series of a priori models based on two criteria: (1) a review of pertinent published literature on *Desmognathus* habitat relations, and (2) evaluation

Table 1 Mean (\pm S.E.) habitat variables for occupied and unoccupied sites by *Desmognathus* salamanders in headwater streams within the Fernow Experimental Forest, Tucker County, West Virginia, June–August 2005. Habitat variables compared between occupied and unoccupied sites using two sample *t*-tests (n = 36)

Habitat variable	Occupied	Unoccupied	t	P	
Cover surface area (cm ²)	621.88 ± 74.12	214.89 ± 14.11 -7.6		< 0.0001	
0.5 m ² plot substrate (%)					
Boulder ^a	6.40 ± 2.27	10.14 ± 2.59	1.59	0.117	
Cobble	52.28 ± 3.33	37.24 ± 3.22	-3.29	0.002	
Gravel	25.56 ± 2.85	31.15 ± 2.90	1.35	0.183	
Silt	15.83 ± 2.63	21.52 ± 3.76	1.13	0.265	
Water (%)	16.00 ± 3.08	25.46 ± 4.49	1.35	0.184	
Cover type (%)					
Rock ^a	92.51 ± 1.63	89.08 ± 2.94	-1.12	0.269	
Coarse woody debris ^a	3.12 ± 1.11	3.76 ± 1.23	0.37	0.713	
Debris ^a	4.38 ± 1.07	7.16 ± 2.42	0.96	0.340	
Embedded substrate (%)	16.87 ± 1.34	29.17 ± 3.81	2.90	0.005	

^a Analysis performed on ranked data.

of our stream habitat results (Russell et al., 2005). We constructed the following five models to predict cutting disturbance abundance effects at the compartment-level: (1) VOLUME (cumulative m³/ha timber removed over 50 year period), (2) ROAD (density (m/ha) of permanent graveled roads within stream watersheds), (3) LASTDISTURB (years since last harvest in compartment), (4) DISTURBANCE (VOLU-ME + ROAD), and (5) GLOBAL (a global model containing all parameters). To describe stream reach-scale habitat effects on Desmognathus abundance, we constructed the following eight models: (1) SUBSTRATE (percent embedded rock + percent cobble + cover object surface area), (2) GRADIENT (percent slope of sampled stream reach), (3) BUFFER (basal area of forest along stream reach), (4) ELEVATION (reach elevation), (5) PH (pH of stream reach sampled), (6) EMBEDDED (percent embedded stream substrate), (7) PHYSICAL (SUB-STRATE + ELEV + PH + SLOPE), and (8) GLOBAL (a global model containing all parameters). Prior to linear regression analyses, we determined that no continuous variables were highly correlated using Spearman's rank correlation with values of $r_s > 0.7$ as thresholds. For partial cutting disturbance models, the time since last disturbance and road density variables were multiplied by -1 and inverse square-root transformed to approximate normality. We ranked all candidate models according to their AICc scores. Although models within 4–7 units of AICcmin are believed to have some empirically-based, explanatory support, we drew primary inference from competing models within two units of AICcmin (Burnham and Anderson, 2002). We evaluated models based on AICcmin differences (\triangle AICc) and Aikaike's weights (w_i). Aikaike weights estimate the probability that a particular model is the best model in the candidate set (Burnham and Anderson, 2002).

3. Results

We observed a total of 426 *Desmognathus* salamanders in the 36, 10 m stream reaches surveyed. Specifically, we recorded

microhabitat data for 138 *D. fuscus* and 88 *D. monticola*. Combined density of *D. fuscus* and *D. monticola* in our sampled streams ranged from 0.27 to 0.98 individuals/m². Captures not included in habitat analyses were eight *G. porphyriticus*, seven *Plethodon cinereus*, and two *E. bislineata*. For *Desmognathus* habitat variables examined, cover surface area and percent cobble cover were greater in occupied plots than in unoccupied plots (Table 1). Conversely, percent embedded rock was greater in unoccupied than in occupied plots (Table 1).

Of the five linear regression models we constructed to explain partial cutting effects at the compartment-level, the best approximating model ($w_i = 0.46$) explaining Desmognathus abundance was VOLUME (Table 2). Salamander abundance decreased with increasing volume/ha of timber removed over 50 years (Table 3). The second-best model, LASTDISTURB, also received strong empirical support ($w_i = 0.36$; Table 2). Our LASTDISTURB model indicated that increasing years since last entry within compartments positively affected Desmognathus abundance (Table 3). Moreover, weight of evidence for the VOLUME model was only 1.28 times greater

Table 2 Linear regression models explaining compartment-level (n = 12) disturbance effects on *Desmognathus* salamander abundance in headwater streams within the Fernow Experimental Forest, Tucker County, West Virginia, June–August 2005. Model rankings were based on Akaike's Information Criterion corrected for small sample size (AICc)

Model ^a	K^{b}	AICc	$\Delta { m AIC}c^{ m c}$	w_i^{d}
VOLUME	3	71.26	0.00	0.46
LASTDISTURB	3	71.72	0.46	0.36
DISTURBANCE	4	74.33	3.07	0.10
ROAD	3	74.91	3.65	0.07
GLOBAL	5	80.41	9.15	0.01

^a See text for model parameter description.

^b Number of estimable parameters + 2 in approximating model.

^c Difference in value between AICc of the current model versus the best approximating model (minimum AICc).

^d Akaike weight. Probability that the current model (*i*) is the best-approximating among those considered.

Table 3 Linear regression parameter estimates explaining *Desmognathus* abundance from partial cutting effects at the compartment-level (n=12) in headwater streams within the Fernow Experimental Forest, Tucker County, West Virginia, June–August 2005

Model	β	S.E.	R^2	Relationship
VOLUME			0.27	_
Intercept	45.13	6.55		
Cumulative timber harvested (m³/ha) ^a	-0.15	0.08		
LASTHARVEST			0.24	+
Intercept	49.13	8.78		
Years since last harvest	42.53	23.84		

^a Variable was negative inverse square-root transformed to approximate normality.

than of the LASTDISTURB model ($w_{\text{volume}}/w_{\text{lastdisturb}}$), suggesting some uncertainty in selection of the best candidate model. The DISTURBANCE and ROAD models also had some empirical support for explaining *Desmognathus* abundance (Table 2).

Of the eight linear regression models we constructed for reach-scale variables, the best approximating model ($w_i = 0.57$) explaining *Desmognathus* abundance was EMBEDDED (Table 4). This model indicated that increased proportion of embedded substrate within streambeds had a negative impact on salamander abundance (Table 5). The PH and SUBSTRATE models also had some empirical support for explaining *Desmognathus* abundance (Table 4).

4. Discussion

Our modeling efforts resulted in the selection of two competing models explaining partial cutting effects on *Desmognathus* abundance. The VOLUME model included the single variable of cumulative timber removal (m³/ha) within silvicultural compartments and suggests that increasing removal of timber volume results in lower salamander

Table 4 Linear regression models explaining stream reach-scale (n = 36) habitat effects on *Desmognathus* salamander abundance in headwater streams within the Fernow Experimental Forest, Tucker County, West Virginia, June–August 2005. Model rankings were based on Akaike's Information Criterion corrected for small sample size (AICc)

Model ^a	K^{b}	AICc	$\Delta { m AIC}c^{ m c}$	w_i^{d}
EMBEDDED	3	152.93	0.00	0.57
SUBSTRATE	5	155.83	2.90	0.13
PH	3	156.65	3.61	0.09
BA	3	157.10	4.17	0.07
GRADIENT	3	157.50	4.57	0.06
ELEVATION	3	157.62	4.70	0.06
PHYSICAL	8	160.15	7.22	0.02
GLOBAL	10	165.11	12.18	0.00

^a See text for model parameter description.

Table 5
Linear regression parameter estimates from stream reach-scale (*n* = 36) models explaining *Desmognathus* abundance at 10-m stream reaches within the Fernow Experimental Forest, Tucker County, West Virginia, June–August 2005

Model	β	S.E.	R^2	Relationship
EMBEDDED			0.12	_
Intercept	18.80	3.45		
Percent embedded substrate ^a	-12.73	5.83		

^a Variable was arcsin square-root transformed to approximate normality.

abundance, supporting our initial hypothesis and similar to the work in New England with *G. porphyriticus* and *E. bislineata* (Lowe and Bolger, 2002; Perkins and Hunter, 2006). However, differences in stream habitat were not compared among treatments in the former nor were differences in cutting practices noted in the latter, thus limiting full comparisons to our work. Adverse impacts on stream habitat associated with timber harvesting, particularly increased sedimentation, are generally greater with increasing timber removal (Kreutzweiser and Capell, 2001), therefore, salamander populations within heavily harvested watersheds may require greater recovery periods to reach pre-disturbance densities. In part, this relationship is attributable to increased sedimentation during harvest events and subsequent recovery of stream habitat as sediments are flushed from streambeds.

Of our eight stream reach-scale models explaining Desmognathus abundance, the best-approximating model included the single variable of the percent of embedded substrate (Table 4). Additionally, our SUBSTRATE model that also included the percent of embedded substrate, received limited empirical support further suggesting that the streams' physical habitat conditions influence Desmognathus abundance. Large substrate (gravel, cobble, and boulders) becomes embedded when fine sediments fill spaces along the vertical surface of the substrate (Lowe and Bolger, 2002; Suttle et al., 2003). Although variable, increases in the proportion of embedded substrate often result from increased deposition of fine sediments in streambeds from upland cutting activities in disturbed forests (Waters, 1995). Interstitial spaces and accessible cover objects are important components of stream habitat for both adult and juvenile Desmognathus (Petranka, 1998; Lowe et al., 2004), to maintain moist conditions for sufficient respiratory exchange and to avoid desiccation particularly during dry ambient conditions (Spight, 1968; Spotila, 1972). Effects on larvae may be exacerbated by changes in pH, as larval Desmognathus are especially susceptible to more acidic conditions (Gore, 1983). Abundance of D. quadramaculatus was positively associated with cobble density in first-order streams in oak (Quercus spp.)-hickory (Carya spp.) forests in the southern Appalachians (Davic and Orr, 1987). Similarly, we observed that Desmognathus in our study occupied larger cover objects relative to unoccupied cover objects. Additionally, the percent of embedded substrate was lower in occupied areas relative to unoccupied areas (Table 1). Sedimentation has been hypothesized as a dominant cause for suppressed stream salamander populations both in the Pacific Northwest (Corn and Bury, 1989; Stoddard and Hayes,

^b Number of estimable parameters + 2 in approximating model.

^c Difference in value between AICc of the current model versus the best approximating model (minimum AICc).

^d Akaike weight. Probability that the current model (*i*) is the best-approximating among those considered.

2005; Ashton et al., 2006) and New England (Lowe and Bolger, 2002; Lowe et al., 2004; Lowe, 2005).

Negative impacts of increased sedimentation resulting from upstream harvest activities on stream amphibians also are well documented in many forested systems (Bury and Corn, 1988; Corn and Bury, 1989; Welsh and Ollivier, 1998; Lowe and Bolger, 2002; Stoddard and Hayes, 2005; Ashton et al., 2006). In the central Appalachians, timber harvesting typically results in some degree of soil disturbance (Weitzman and Trimble, 1955; Patric, 1976, 1980; Kochenderfer, 1977). In the short term, this can result in greater silt runoff to streams (Aubertin and Patric, 1974; Kochenderfer et al., 1987, 1997). However, increased sedimentation levels associated with harvesting activities are believed short-lived, and negligible within a few years following initial disturbance if proper erosion control methods are used, such as carefully planned skid roads in the region (Reinhart et al., 1963). Nonetheless, repeated cutting entries within a short time period could produce a "chronic" effect by intermittently supplying low-level inputs of sedimentation into streambeds through increased skid road density before previous inputs are flushed.

Because water flow in headwater Appalachian streams is controlled largely by precipitation, most streams have limited capacity to flush large amounts of sediments transported in through periodic flood events (Kochenderfer et al., 1997). A few large storm events produce heavy flows that can transport the majority of streams' annual sediment inputs. However, these events generally flush this sediment, and previously stored sediment, downstream. Conversely, moderate storms transport sediment into stream channels but lack the force to flush stored sediments downstream, thereby allowing it to accumulate in the streambed (Kochenderfer et al., 1997). Although our road density estimates for watersheds were overly conservative in that they did not include the temporary skid roads used during harvesting that produce the majority of sediment inputs (Waters, 1995), the ROAD and DISTURBANCE models, both including the road density variable, received some empirical support. Accumulation of sediments may be exacerbated by increased skid road density associated with extensive harvest events resulting in a greater proportion of embedded substrate within streambeds. Disturbance resulting in reduced availability of or access to large cover objects may reduce the ability of headwater streams to sustain high Desmognathus densities.

Desmognathus can often occur at high densities in undisturbed Appalachian stream habitats (Petranka, 1998). Hall (1977) estimated 0.74/m² D. fuscus occurring in central Appalachian streams and Kleeberger (1984) reported a range of 0.72–1.4/m² for D. monticola in similarly optimal conditions in the southern Appalachians. Conversely, in disturbed land-scapes, Desmognathus densities are reduced or even extirpated (Orser and Shure, 1972; Willson and Dorcas, 2003; Price et al., 2006). For example, many streams within heavily urbanized areas of the Piedmont in the southeastern United States support either low densities of D. fuscus or had experienced extirpation

due to expansive agricultural and urban development within many watersheds (Orser and Shure, 1972; Price et al., 2006). Still, many of these types of landscape change represent more drastic, if not permanent forms, of disturbance relative to the partial cutting conditions we examined. Nonetheless, we observed that mean Desmognathus density was approximately 30% higher in streams within mature second-growth undisturbed over the past 90 years as compared to streams in disturbed compartments. Although we lack preharvest data for salamander abundances, suppressed Desmognathus densities in harvested stands likely reflect long-term cutting impacts. The long duration of partial cutting activities within our study compartments should account for any population lag associated with disturbance including unsuccessful reproduction and/or delayed immigration of resident individuals. However, persistence of Desmognathus, albeit at reduced densities, within disturbed compartments suggests that headwater stream Desmognathus populations in central Appalachian mixedmesophytic forests do demonstrate some tolerance to long-term partial cutting.

5. Conclusion

Currently, West Virginia BMP guidelines recommend a 30.5 and 7.6 m forested buffer zone around intermittent/ perennial and ephemeral streams, respectively (West Virginia Department of Natural Resources, 2006). The ability of these buffers to reduce stream sedimentation following forest harvesting activities has been demonstrated conclusively in the region (Kochenderfer et al., 1997; Kochenderfer and Hornbeck, 1999). Although adherence to BMP's in West Virginia, particularly use of streamside management zones (SMZ's) is increasing, regulatory guidance on appropriate road and landing layouts is lacking (Wang et al., 2004). This is of particular concern because skid road density increases with increasing partial cutting intensity (Kochenderfer, 1977). Therefore, planning efforts should focus on proper skid road and landing placement and maintenance to minimize sediment input into streams (Kreutzweiser and Capell, 2001).

Our study indicates that Desmognathus salamander abundance in West Virginia headwater streams has responded negatively over time to habitat degradation from increased sedimentation resulting from timber harvesting. Stream habitat degradation is often associated with declines in long-lived, keystone species, such as stream salamanders (Odum, 1985). In the near-term, density reduction of *Desmognathus* can result in increased prey species density and biomass, and subsequent shifts in invertebrate community composition and allochthonous input retention (Davic, 1983; Davic and Welsh, 2004). Although our results indicate that impacts of partial cutting practices do not threaten long-term viability of Desmognathus populations per se, further investigations concerning how reduced abundance of these predators affects prey species diversity, trophic cascades, nutrient cycling, and resistanceresilience pathways in central Appalachian headwater stream does seem warranted.

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References

- Allan, J.D., 1995. Stream Ecology: Structure and Function of Running Waters. Chapman and Hall, London.
- Ashton, D.T., Marks, S.B., Welsh Jr., H.H., 2006. Evidence of continued effects from timber harvesting on lotic amphibians in redwood forests of northwestern California. For. Ecol. Manage. 221, 183–193.
- Aubertin, G.M., Patric, J.H., 1974. Water quality after clearcutting a small watershed in West Virginia. J. Environ. Qual. 3, 243–249.
- Barbour, R.W., Hardin, J.W., Schafer, J.P., Harvey, M.J., 1969. Home range, movements, and activity of the dusky salamander, *Desmognathus fuscus*. Copeia 293–297.
- Barthalamus, G.T., Bellis, E.D., 1972. Home range, homing and the homing mechanism of the salamander. *Desmognathus fuscus*. Copeia 632–642.
- Burnham, R.B., Anderson, D.R., 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.
- Bury, R.B., Corn, S., 1988. Responses of aquatic and streamside amphibians to timber harvest: a review. In: Raedeke, K.J. (Ed.), Streamside Management: Riparian Wildlife and Forestry Interactions, Proceedings of the Symposium, February 11–13, 1987, University of Washington, Seattle, pp. 165–181.
- Corn, P.S., Bury, R.B., 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. For. Ecol. Manage. 29, 39–57.
- Corn, P.S., Bury, R.B., Hyde, E.J., 2003. Conservation of North American stream amphibians. In: Semlitsch, R.D. (Ed.), Amphibian Conservation. Smithsonian Institute Books, Washington D.C., pp. 24–36.
- Davic, R.D., 1983. An Investigation of Salamander Guild Predation in a North Carolina Stream: An Experimental Approach. Ph.D. Dissertation. Kent State University.
- Davic, R.B., Orr, L.P., 1987. The relationship between rock density and stream salamander density in a mountain stream. Herpetologica 43, 357–361.
- Davic, R.B., Welsh Jr., H.H., 2004. On the ecological roles of salamanders. Annu. Rev. Ecol. Evol. Syst. 35, 405–434.
- de Maynadier, P.G., Hunter Jr., M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environ. Rev. 3, 230–261.
- Duguay, J.P., Wood, P.B., 2002. Salamander abundance in regenerating forest stands on the Monongahela National Forest West Virginia. For. Sci. 48, 331–335
- Fajvan, M.A., Grushecky, S.T., Hassler, C.C., 1998. The effects of harvesting practices on West Virginia's wood supply. J. Forestry 96, 33–39.
- Fajvan, M.A., 2006. Research on diameter-limit cutting in central Appalachian forests. In: Kenefic, L.S., Nyland, R.D. (Eds.), Proceedings of the Conference on Diameter-Limit Cutting in Northeastern Forests. USFS General Technical Report NE-34, pp. 32–38.
- Ford, W.M., Menzel, M.A., McCay, T.S., Gassett, J.W., Laerm, J., 2000. Woodland salamander and small mammal responses to alternative silvicultural practices in the southern Appalachians of North Carolina. In: Proc. Ann. Conf. Southeast. Assoc. Fish and Wildl. Agencies 54. pp. 241–250.
- Ford, W.M., Chapman, B.R., Menzel, M.A., Odom, R.H., 2002. Stand age and habitat influences on salamanders in Appalachian cove hardwood forests. For. Ecol. Manage. 155, 131–142.
- Fredericksen, T.S., Ross, B.D., Hoffman, W., Ross, E., Morrison, M.L., Beyea, J., Lester, M.B., Johnson, B.N., 2000. The impact of logging on wildlife: a study in northeastern Pennsylvania. J. Forestry 98, 4–10.
- Gordon, N.P., McMahon, T.A., Finlayson, B.L., 1992. Stream Hydrology: An Introduction for Ecologists. Wiley, New York.

- Gore, J.A., 1983. The distribution o Desmognathine larvae (Amphibia: Plethodontidae) in coal surface mine impacted streams of the Cumberland Plateau, USA. J. Fresh. Ecol. 2, 13–23.
- Hairston, N.G., 1987. Community Ecology and Salamander Guilds. Cambridge University Press, Cambridge.
- Hall, R.J., 1977. A population analysis of two species of streamside salamanders, Genus Desmognathus. Herpetologica 33, 109–113.
- Harpole, D.N., Haas, C.A., 1999. Effects of seven silvicultural treatments on terrestrial salamanders. For. Ecol. Manage. 114, 349–356.
- Kleeberger, S.R., 1984. A test of competition in two sympatric populations of Desmognathine salamanders. Ecology 65, 1846–1856.
- Knapp, S.M., Haas, C.A., Harpole, D.N., Kirkpatrick, R.L., 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. Conserv. Biol. 17, 752–762.
- Kochenderfer, J.N., 1977. Area in skidroads, truck roads, and landings in the Central Appalachians. J. Forestry 75, 507–508.
- Kochenderfer, J.N., Helvey, J.D., Wendel, G.W., 1987. Sediment yield as a function of land use in central Appalachian forests. In: Proc. Sixth Central Hardwood Conference. pp. 497–501.
- Kochenderfer, J.N., Edwards, P.J., 1990. Effectiveness of three streamside management practices in the Central Appalachians. In: Proc. Sixth Southern Silvicultural Research Conference. pp. 688–700.
- Kochenderfer, J.N., Edwards, P.J., Wood, F., 1997. Hydrologic impacts of logging an Appalachian watershed using West Virginia's best management practices. North. J. Appl. For. 14, 207–218.
- Kochenderfer, J.N., Hornbeck, J.W., 1999. Contrasting timber harvest operations illustrate the value of BMPs. In: Stringer, J.W., Loftis, D.L. (Eds.), Proceedings of the 12th Central Hardwood Conference, Lexington, KY, February 28–March 2, 1999, USFS General Technical Report SRS-24, pp. 128–135.
- Kreutzweiser, D.P., Capell, S.S., 2001. Fine sediment deposition in streams after selective forest harvesting without riparian buffers. Can. J. For. Res. 31, 2134–2142.
- Lowe, W.H., Bolger, D.T., 2002. Local and landscape-scale predictors of salamander abundance in New Hampshire headwater streams. Conserv. Biol. 16, 183–193.
- Lowe, W.H., Nislow, K.H., Bolger, D.T., 2004. Stage-specific and interactive effects of sedimentation and trout on a headwater stream salamander. Ecol. Appl. 14, 164–172.
- Lowe, W.H., 2005. Factors affecting stage-specific distribution in the stream salamander *Gyrinophilus porphyriticus*. Herpetologica 61, 135–144.
- Madarish, D.M., Rodrigue, J.L., Adams, M.B., 2002. Vascular Flora and Macroscopic Fauna on the Fernow Experimental Forest. USFS General Technical Report NE-291.
- Miller, G.W., 1993. Financial Aspects of Partial Cutting Practices in central Appalachian Hardwoods. USFS Research Paper NE-673.
- Odum, E.P., 1985. Trends expected in stressed ecosystems. Bioscience 35, 419–422.
- Orser, P.N., Shure, D.J., 1972. Effects of urbanization on the salamander Desmognathus fuscus fuscus. Ecology 53, 1148–1153.
- Patric, J.H., 1976. Soil erosion in eastern forests. J. Forestry 74, 671-676.
- Patric, J.H., 1980. Effects of wood products harvest on forest soil and water relations. J. Environ. Qual. 9, 73–80.
- Perkins, D.W., Hunter Jr., M.L., 2006. Effects of riparian timber management on amphibians in Maine. J. Wild. Manage. 70, 657–670.
- Petranka, J.W., 1983. Fish predation: a factor affecting the spatial distribution of a stream-dwelling salamander. Copeia 1983, 624–628.
- Petranka, J.W., 1998. Salamanders of the United States and Canada. Smithsonian Institute Press, Washington D.C..
- Petranka, J.W., Smith, C.K., 2005. A functional analysis of streamside habitat use by southern Appalachian salamanders: implications for riparian forest management. For. Ecol. Manage. 210, 443–454.
- Price, S.J., Dorcas, M.E., Gallant, A.L., Klaver, R.W., Willson, J.D., 2006. Three decades of urbanization: estimating the impacts of land-cover change on stream salamander populations. Biol. Cons. 133, 436–441.
- Reinhart, K.G., Eschner, A.R., Trimble Jr., G.R., 1963. Effect on Streamflow of Four Forest Practices in the Mountains of West Virginia. USFS Research Paper NE-1.

- Russell, K.R., Mabee, T.J., Cole, M.B., Rochelle, M.J., 2005. Evaluating biotic and abiotic influences on torrent salamanders in managed forests of western Oregon. Wildlife Soc. Bull. 33, 1413–1424.
- SAS Version 9.1, 2003. SAS Institute Inc., Cary, NC, USA.
- Schuler, T.M., Gillespie, A.R., 2000. Temporal patterns of woody species diversity in a central Appalachian forest from 1856 to 1997. J. Torrey Bot. Soc. 127, 149–161.
- Schuler, T.M., 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. Can. J. For. Res. 34, 985–997
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The Practice of Silviculture: Applied Forest Ecology. Wiley and Sons, New York.
- Smith, C.K., Petranka, J.W., 2000. Monitoring terrestrial salamanders: repeatability and validity of area-constrained cover object searches. J. Herp. 34, 547–557
- Smith, S., Grossman, G.D., 2003. Stream microhabitat use by larval two-lined salamanders (Eurycea cirrigera) in the Georgia Piedmont. Copiea 531–543.
- Sokal, R.R., Rohlf, F.J., 1987. An Introduction to the Study of Biostatistics. W.H. Freeman and Company, New York.
- Spight, T.M., 1968. The water economy of salamanders: evaporative water loss. Physiol. Zool. 41, 195–203.
- Spotila, J.R., 1972. Role of temperature and water in the ecology of lungless salamanders. Ecol. Monogr. 42, 95–125.
- Stoddard, M.A., Hayes, J.P., 2005. The influence of forest management on headwater stream amphibians at multiple spatial scales. Ecol. Appl. 15, 811–823

- Stuart, G.W., Edwards, P.G., 2006. Concepts about forests and water. North J. Appl. For. 23, 11–19.
- Suttle, K.B., Power, M.E., Levine, J.M., McNeely, C., 2003. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecol. Appl. 14, 969–974.
- Trimble Jr., G.R., 1977. A history of the Fernow Experimental Forest and the Parsons Timber and Watershed Laboratory. USFS General Technical Report NE-28.
- Wang, J., McNeel, J., Milauskas, S., 2004. Logging sediment control act and forestry best management practices in West Virginia: a review. North J. Appl. For. 21, 93–99.
- Waters, T.F., 1995. Sediment in Streams: Sources, Biological Effects, and Control. American Fisheries Society Monograph 7, Bethesda, MD.
- Weitzman, S., Trimble Jr., G.R., 1955. Integrating timber and watershed management in mountain areas. J. Soil. Water Conserv. 10, 70–75.
- Welsh Jr., H.H., Ollivier, L.M., 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. Ecol. Appl. 8, 1118–1132.
- Welsh Jr., H.H., Droege, S., 2001. A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. Conserv. Biol. 15, 558–569.
- West Virginia Department of Natural Resources, 2006. West Virginia Silvicultural Best Management Practices for Controlling Soil Erosion and Sedimentation from Logging Operations.
- Willson, J.D., Dorcas, M.E., 2003. Effects of habitat disturbance on stream salamanders: implications for buffer zone and watershed management. Conserv. Biol. 17, 763–771.